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# THE SPERMATOGENESIS OF ONISCUS ASELLUS LINN., WITH ESPECIAL REFERENCE TO THE HISTORY OF THE CHROMATIN.

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THIS study was begun in February, 1899, and finished in January, 1901. Its more important results are described in this paper. A more complete and detailed account of the spermatogenesis will appear in a later publication.

## I. STRUCTURE OF THE TESTIS.

Each one of the two testes consists of three narrow lobes, distinct from one another and opening successively into the anterior expanded portion of the vas deferens. The interior of each lobe or follicle is occupied by the germ cells, which are in differing stages of development in the three follicles of one side. Each follicle may be divided into two principal regions of growth, composed of cells of different generations and of differing degrees of development. The illustration (Fig. 1) will make this clear.[1] It shows, in a typical case, the comparative degrees of development to which the cells of the three follicles have attained. Thus, in the most posterior of the

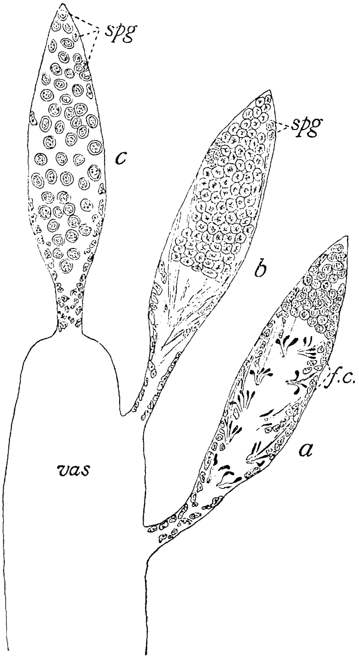

FIG. 1. — Testis of *Oniscus asellus* Linn. *a, b, c,* follicles of testis; *vas,* anterior part of vas deferens; *f.c.,* follicle cells; *spg,* spermatogonia.

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[1] This and the following figures are slightly schematic.

follicles (*a*) the apical third is occupied exclusively by spermatogonia, some of which can be seen in mitosis ; the basal region, on the other hand, by spermatids in an immature state. Follicle cells occur on the outside of the follicle, being especially abundant in the basal region. In the adjacent follicle (*b*) the apical two-thirds is occupied by cells in the synapsis stage, the remaining portion by spermatids in a stage of development later than that of follicle (*a*). Along the margin of the follicle are found scattered small groups of spermatogonia (*spg*). The third and most anterior follicle (*c*) contains chiefly spermatocytes in a late prophase. Groups of spermatogonia similar to those of follicle (*b*) are here also found scattered along the margin and nearly filling the extreme apical portion. The follicle cells in the basal region are undergoing not only active amitotic division, but to a certain extent degeneration. Their active multiplication or fragmentation causes them to crowd in towards the axis of the follicle.

From a comparison of the extent of these growth regions in the three follicles, the developmental cycle may be conceived somewhat as follows. The spermatozoa, when fully formed, are forced into the vas. Since they have no motion of their own, this is probably caused by the contraction of the muscle layer of the follicle, perhaps assisted by the pressure of the growing cells in the apical region. During this process the spermatogonia in the apical portion of the follicle divide and come to fill up the space left vacant by the discharged sperm. The majority of the spermatogonia thus filling up the follicle proceed in their development, while the remainder form the groups of cells along the margin of the follicle already described in follicles (*b*) and (*c*), and which are destined to supply a new generation of cells. The spermatids also proceed in development and are forced into the vas.

A condition like that represented in follicle (*b*) thus arises, the basal region filled with spermatozoa in a late stage about to pass into the vas deferens, and the apical region with cells which have progressed as far as the synapsis stage. Later, the spermatozoa having been completely discharged, the cells of the apical region come to occupy the basal part of the follicle, being now less compactly pressed together (*c*). Their development progresses until, having become mature spermatozoa, they pass into the vas deferens ; the spermatogonia again fill the apical region and the cycle is repeated.

## II. Spermatogenesis.

### 1. *Maturation.*

The chief feature of interest in the history of the chromatin lies in the fact that the first maturation division separates univalent chromosomes and is therefore reducing.

This can be demonstrated by following the changes in the chromosomes from the synapsis stage through the first maturation division. In the anaphase of the last spermatogonic division the chromatin threads lie massed together near the center of the cell so as to be almost indistinguishable from each other. They gradually spread apart and are seen to be for the most part V-shaped (Fig. 2 *a*). There follows an elongation of the threads, and during this process the granules of which they are composed divide into two, so that each chromosome becomes longitudinally split (Fig. 2 *b*). Of the entire number of chromosomes present it is difficult to be certain, owing to the fact that they overlie each other so closely. The number, however, is certainly less than that present in the spermatogonia and not greater than sixteen. The reduction in the number of the chromosomes apparently takes place, therefore, at this stage, and the V-shape so prevalent is due to the approximation of two of the spermatogonic chromosomes to form a bivalent one. The threads become more and more attenuated, and finally by anastomosis are transformed into the nuclear reticulum of the resting spermatocyte. The fact that the chromosomes remain distinct until just before the formation of the nuclear membrane points to a maintenance of their individuality in the resting cell. In preparing for the first maturation division, the meshes of the nuclear network become coarser, the granules

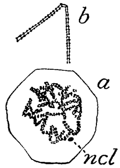

FIG. 2.—*a*, cell in the synapsis stage. *b*, bivalent chromosome at a later period of the synapsis, showing the longitudinal splitting of the chromatin granules ; *ncl*, nucleolus.

more distinct and aggregated into separate threads joined together by linin. The manner of their origin again lends support to the view concerning their individuality in the resting cell. By a gradual process of condensation sixteen compact masses of chromatin are produced. These sixteen masses are of various forms. Some are dumb-bell-shaped, two spheres of chromatin joined together by linin ; some are crescent-shaped, and still others are more or less complete rings (Fig. 3). The different forms may occur in the same nucleus, but apparently without constancy in the ratio of relative frequency of occurrence.

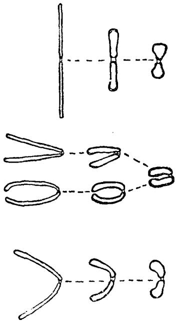
FIG. 3.—Mode of formation of the bivalent spermatocytic chromosomes (diagrammatic).

Two main types may be distinguished among the chromosomes according to their structure and mode of origin ; *i.e.*, (1) those in which the bivalent chromosome consists of two univalent chromosomes lying end to end, as in those having the dumb-bell shape ; and (2) those in which the univalent chromosomes lie side by side, as in those arising through a ring or narrow V-shape. A form intermediate between these is represented by those having a crescent shape. The different types and their probable mode of origin are shown in the diagram (Fig. 3).

In the equatorial plate of the first maturation division the two forms may again be seen. In sections stained with iron hæmatoxylin and strongly decolorized a longitudinal split is distinguishable in the chromosomes. In the dumb-bell-shaped chromosomes this lies parallel to the long axis of the spindle, but in the others more or less oblique to it, or at right angles to it (Fig. 4). In the spermatogonic divisions, on the contrary, as is shown in preparations similarly treated, the longitudinal split lies transversely to the long axis of the spindle (Fig. 5). Karyokinesis separates originally distinct chromosomes, and the first maturation division is therefore reducing. In many cases the chromosomes can be seen to be composed of a

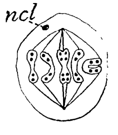

FIG. 4.—Equatorial plate of the first spermatocytic division. *ncl*, nucleolus.

double row of four granules. After division the halves consist of a double row of two granules, or four in all, and thus simulate tetrads.

The true nature of the second maturation division, whether equational or reductional, is difficult to decide, because the length and the breadth of the chromosomes are approximately equal. Since most writers on the maturation of the germ cells in the arthropods agree in ascribing to them both methods of division (equation and reduction), it is probable that since the first division is reducing, the second is equational in Oniscus.

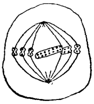

FIG. 5. — Equatorial plate of a spermatogonic division.

These results do not agree with those obtained by Rückert[1] and vom Rath[2] in the ovogenesis of the copepods. The case of Cyclops as described by Rückert is particularly clear. According to his observations the first maturation division is equational, the second reducing. If Rückert's interpretation of the method of reduction in Cyclops be correct, and my own concerning reduction in Oniscus be equally so, it becomes clear that the cell generation in which the true reduction takes place need not be the same for all members of a given class of animals.

## 2. *Metamorphosis of the Spermatids.*

The transformation of the spermatids of the isopods has already been described by Gilson[3] in his comprehensive work on the

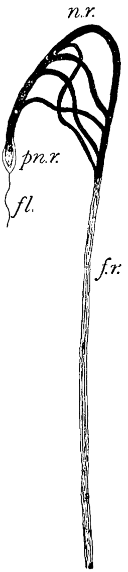

FIG. 6. — Anterior portion of mature sperm colony (less highly magnified). *fl.*, flagellum; *pn.r.*, prenuclear region; *n.r.*, nuclear region; *f.r.*, region of cytoplasmic fibres.

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[1] Rückert, J. Die Chromatinreduktion der Chromosomenzahl im Entwicklungsgang der Organismen, *Merk. u. Bon. Erg.*, Bd. iii, 1893.

*Id.* Zur Eireifung bei Copepoden, *Merk. u. Bon. Erg.*, Anat. Heft, 1894.

[2] Vom Rath, O. Neue Beiträge zur Frage der Chromatinreduktion in der Samen- und Eireife, *A. M. A.*, 46, 1895.

[3] Gilson G. Spermatogénèse chez les Arthropodes, *La Cellule*, 1884 and 1886, tomes i and ii.

spermatogenesis of the arthropods. In some respects my observations agree with his; in others they differ.

The nuclei of the spermatids in Oniscus undergo a gradual elongation and condensation. During this process the cell walls between adjacent spermatids disappear and groups of nuclei are formed lying in a common plasma. Within the latter arise bundles of fibres of great length. Gilson in his Fig. 320 shows a direct continuity of these cytoplasmic fibrils with the elongated nuclei. That such a connection actually exists I have been unable to convince myself. In addition to the bundle of fibres there are single fibres of greater delicacy which are continuous with the nuclei. The appearance of the mature sperm colony may be seen from Fig. 6. Figs. 7 and 8 represent longitudinal and transverse sections of immature colonies. With Wilcox's double stain of saffranin and malachite green the cytoplasmic fibres stain green and are thus sharply differentiated from the nuclei, which stain red. In cross-section the nuclei are seen as a circle of red dots surrounding a group of green dots, the cytoplasmic fibrils. In examining a series of sections from the nuclear region towards the flagellum, the group of green dots in the center eventually ceases to be visible, and the surrounding red dots gradually merge into converging green fibres of great delicacy (Figs. 7 and 8). The evidence at my disposal admits of two interpretations, — either the long bundle of cytoplasmic fibres stops abruptly before the anterior end of the bundle is reached, and they thus have no connection with the nuclei, or the connection is of such a character as to escape observation. Since the structures concerned are extremely minute and delicate, the latter might easily be the case.

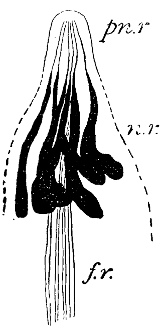

FIG. 7. — Longitudinal section of the anterior portion of an immature sperm colony. *pn.r.*, prenuclear region; *n.r.*, nuclear region; *f.r.*, region of cytoplasmic fibres.

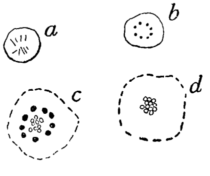

FIG. 8. — Cross-section of immature sperm colony. *a*, prenuclear region; *b* and *c*, nuclear region; *d*, region of cytoplasmic fibres.

## III. SUMMARY.

The main results of this study may be briefly summarized as follows:

1. The spermatogonic chromosomes are joined together in pairs in the synapsis to form sixteen bivalent chromosomes.

2. A longitudinal splitting of the thread takes place at this stage.

3. The distinctness maintained by the chromosomes up to the formation of the nuclear network of the resting spermatocyte and the manner of origin of the spermatocytic chromosomes from it lends support to the theory of their individuality in the resting nucleus.

4. In the structure and mode of origin of the bivalent chromosomes two main types may be distinguished: (*a*) the component chromosomes lie end to end, or (*b*) they lie side by side.

5. Inasmuch as univalent chromosomes are separated, the first maturation division is reducing.

6. Sphere substance (idiozome) is not observable, except for a short time during the prophases of the first spermatocyte.

7. The nucleolus of the spermatogonia disappears shortly after dissolution of the nuclear membrane, while that of the spermatocytes, first discovered in the synapsis, persists throughout the divisions.

8. The spermatids become associated in groups to form colonies of nuclei lying in a common plasma.

9. Within the latter arise bundles of fibres of great length, whose connection with the nuclei could not be demonstrated,[1] as well as single fibres of greater delicacy which are continuous with the nuclei.

10. The mature sperm colony consists of a variable number of filamentous nuclei contained, together with the bundle of cytoplasmic fibres, in a tenuous sheath which is flagellate at its anterior extremity.

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[1] If such a connection is actual, it is slight and occurs very late.

I wish to express here sincere gratitude to my instructors, Dr. E. G. Conklin and Dr. Thomas H. Montgomery, Jr., for the valuable advice which has aided me in bringing this work to a successful completion.

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